THE EFFECTS OF MALE *DENDROBATES PUMILIO* REMOVAL ON THE TERRITORIAL BEHAVIOR OF LOCAL MALES

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Abstract. *Dendrobates pumilio* males actively defend territories in order to attract mates. Assuming that male density is limited by resource availability and that males maximize territory size, we hypothesized that removal of a territorial male would result in either territory replacement or expansion of neighboring male territories. We further hypothesized that in regions of low density, removal would result in decreased incidence of territorial replacement and decreased territory expansion by neighbors. We found that the territorial fidelity of *D. pumilio* males was low. Replacement following removal occurred in only one out of nine cases, and we found no trend in territorial expansion. Our results may be due to a decrease in territorial behavior during the dry season when reproductive activity is reduced.

INTRODUCTION (NEP)

Wilbur (1980) suggested that the size of breeding populations of adult frogs may be regulated by male territorial behavior. Intra-male competition for territories may limit the reproductive success of *Dendrobates pumilio*, the poison dart frog. Males choose territories based on reproductive resource availability (Donnelly 1989) and actively defend these sites in order to attract mates. Donnelly (1989) showed that availability of these resources (i.e., bromeliads as tadpole rearing sites) limit *D. pumilio* density. Large territories may offer a greater availability of resources and may be more attractive to potential mates.

Assuming that *D. pumilio* male territories are limited by resource availability and that males maximize territory size, we hypothesized that removal of a *D. pumilio* male would result in either territory replacement by another male or expansion of neighboring male territories. Assuming territory size is influenced by frog density, we hypothesized that in regions of low male density, male *D. pumilio* removal would result in decreased incidence of territory replacement and decreased territory expansion.

METHODS (JLM)

Our study was conducted at La Selva Biological Station, Costa Rica. Experimental manipulations and observations were made on 13 to 15 February 1995 between 0700 and 1100, when *D. pumilio* males call most actively. On the first day of the study, we removed four focal calling males from their territories and marked their perches. The following day we returned to these perches to determine if replacement had occurred. We listened for calling for at least 10 minutes in each territory, and then visually examined the area for male frogs. A replacement was scored if another calling male was found within 1 m of the original perch. On the same morning, we removed five more territorial males (and mapped all neighboring males within a 5 m radius of the (removed) focal male. The local density of males was defined as the number of males within the 5 m radius. Distances and angles between neighbors and focal males were measured. This mapping procedure was also applied to four control focal males, which were not removed from their territories.

On the third day of the study, we returned to this second set of male territories and determined whether replacement had occurred using the same procedure as the first four experimental

males. We also re-mapped all neighboring males. To examine whether neighboring males' territories expanded following focal frog removal we calculated (1) change in distance to nearest neighbor following the removal, and (2) change in mean distance to all males within the 5 m radius following removal.

TABLE 1: Territorial fidelity of control males and change in nearest neighbor and mean neighbor distances between days 1 and 2. (Negative values indicate decrease in distance to neighbors, positive values indicate increase in distance to neighbors)
*NC=No Change, D=Decrease, I=Increase

Frog Number	Density of males (number of males within 5 m radius of focal male)	Presence of focal male on day 2	Change in distance to nearest neighbor (cm)*		Change in mean distances to near neighbors (cm)*	
Control 1	0	Yes	< -220	D	-220	D
Control 2	2	No	-10	D	-27	D
Control 3	1	No	+130	I	+130	I
Control 4	0	No	< -420	D	-420	D

TABLE 2: Presence of replacement males and change in nearest neighbor and mean neighbor distances following focal male removal. (Negative values indicate decrease in distance to neighbors, positive values indicate increase in distance to neighbors)
*NC=No Change, D=Decrease, I=Increase

Frog Number	Density of males (number of males within 5 m radius of focal male before removal)	Presence of replacement male on day 2	Change in distance to nearest neighbor (cm)*		Change in mean distance to near neighbors (cm)*	
Experimental 1	—	No	—	—	—	—
Experimental 2	—	No	—	—	—	—
Experimental 3	—	Yes	—	—	—	—
Experimental 4	—	No	—	—	—	—
Experimental 5	4	No	0	NC	+207	I
Experimental 6	0	No	0	NC	0	NC
Experimental 7	0	No	< -98	D	< -45	D
Experimental 8	2	No	>+205	I	>+127	I
Experimental 9	3	No	+59	I	-65	D

RESULTS

Due to small sample size, we conducted no statistical analysis. Only 1 of 4 control males was found at the same perch the day after initial observation (Table 1). Additionally, nearest neighbor distances to control males were not constant between the two observation days.

Replacement was observed in 1 of 9 removals. Although we did not assess initial neighbor distances from this individual, we noted that this site contained a high density of calling males.

Distance between nearest neighbor and focal male as well as mean neighbor distance from focal male were compared before and after removal. We found no consistent trend in change in nearest neighbor or mean neighbor distances from focal males (Table 2). In addition, there was no apparent relationship between local male density, replacement, and territorial expansion.

DISCUSSION

We formulated our hypotheses based on the assumption that calling *D. pumilio* males establish stable territories. The lack of territorial fidelity in control sites indicates that this assumption may be invalid. A possible reason for this

territorial instability is that although both males and females are reproductively active throughout the year, breeding is concentrated during the wet season (Donnelly 1989). If males maintain territories to defend reproductive resources but not food resources (Donnelly 1983), territories might only function to increase male reproductive success by attracting females. During the dry season, when breeding activity is reduced, there may be less incentive for males to maintain territories.

Territory replacement may be a function of territory availability. If the importance of male territoriality decreases in the dry season, the abundance of available territories may not be limiting and replacement may occur less frequently. The time limitations of our study could also be a factor in the low incidence of territorial replacement. More than one day may be required for males without territories to encounter uninhabited territories and establish residence. In addition, more time may be required for neighboring male territory holders to assess the quality and availability of the vacated territory.

The single replacement occurred in a plot with a high density of territorial males. In areas of high male density, encounter rates of uninhabited territories may be higher than in areas of low density. Regions of high male density might also indicate a greater abundance of desirable resources. If so, the incidence of replacement may be higher in regions of high male density.

The absence of any trend in neighboring male territory expansion following removal may also be a result of decreased breeding activity in the dry season. The increased costs of defending a larger territory might not be offset by increased breeding success.

Future studies should investigate potential changes in male *D. pumilio* territorial behavior between wet and dry seasons. Decreased territorial behavior during the dry season may lend support to the hypothesis that the level of reproductive activity influences territoriality of *D. pumilio* males.

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